Visual imagery vividness and mental rotation of characters

Visual imagery vividness and mental rotation of characters: an event related potentials study

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Word count: 5,957

Abstract

Recent behavioural evidence suggests that differences in the vividness of visual imagery (VVI) affect the way in which mental rotation (MR) tasks are accomplished. However, the role of VVI in MR tasks is still debated. We explored it using event-related brain potentials (ERPs) which allow to track the time course of MR processes with high temporal resolution. We assigned participants to two different groups based on their VVI and compared the rotation-related negativity (RRN), the electrophysiological correlate of MR. Accuracy did not differ in the two groups. However, the RRN offset was delayed in lower as compared to higher VVI individuals. The processing of MR as indexed by the RRN is longer in individuals with lower VVI, providing direct evidence for a role of VVI in MR processing.

Key words: visual imagery vividness (VVI); mental rotation; individual differences; rotation-related negativity (RRN); RRN onset-offset

Introduction

Mental rotation (MR) tasks have been widely used to assess mental imagery. In the classic MR task [1], participants are presented with pairs of visual stimuli with different rotation angles and asked to report whether these are identical or mirror images of one another. Response times (RTs) increase linearly with the increasing rotation angles. This linear increment in RTs suggests that participants create an image of the object in their mind's eye and then rotate it in a process akin to the actual physical rotation of the object (e.g. [1], [2], [3]).

This ability to create and transform visual mental representations varies considerably across individuals [4] [5]. The vividness of visual imagery (VVI) has been suggested to impact the strategy used to perform mental operations on the visual representation of stimuli (e.g. [6], [7], [8]). A recent behavioural study [6] showed differences between individuals with higher and lower imagery vividness when they were asked to perform a MR of complex but not simple stimuli. Individuals with higher but not those with lower VVI were able to simplify the mental visual representations of complex stimuli for further MR processing, as revealed by shallower MR slopes of the regression function relating RTs to rotation angles (MR slopes of RTs), when they rotated complex as compared to simpler stimuli. However, other studies have failed to observe such differences (e.g. [9], [10]).

Behavioural measures alone might not be sufficient to detect individual differences in MR because they reflect the end result of several different cognitive sub-processes (i.e., character processing, character identification, MR proper, parity judgment and response selection and execution) [11]. Imaging techniques can provide a more direct insight into the cognitive processes underlying MR [12], [13], [14] and might be more sensitive to individual differences. A recent fMRI study of MR, showed that individuals with different levels of VVI had similar

behavioural performances yet recruited different brain areas [7], suggesting that the VVI affected the way in which the mental representations of stimuli were transformed.

No study to date has compared electrical brain activity measured during a MR task in individuals with higher and lower VVI. Electrophysiological measures can track the time course of cognitive processes with higher temporal resolution, and can differentiate between different cognitive processes. In particular, the 'Rotation Related Negativity' (RRN) is typically elicited over parietal brain regions during MR tasks in which participants have to mentally rotate alphanumeric characters approximately between 350-650ms after stimulus onset [15], [16], [17], [18]. This ERP component is considered the electrophysiological correlate of MR proper because its amplitude becomes more negative with increasing rotation angles and its onset is delayed when the initial stimulus encoding phase takes longer (e.g., [11]). To assess whether individual differences in VVI are associated with differences in the electrophysiological correlate of MR, in the current study participants were grouped according to their scores on a VVI questionnaire [5] and performed a letter rotation task [19], [20].

A recent ERP study [21] showed larger RRN amplitudes across angles for low- compared to high-performers (grouped by a median split of error rates). It was suggested that these larger RRN amplitudes observed in low-performers reflected an increase of MR effort to cope with the MR task (i.e., the neural efficiency hypothesis, [22]). Thus, if individuals with lower VVI perform worse than those with higher VVI in the letter rotation task of the present study, a larger RRN amplitude is expected. However, existing behavioural and fMRI studies have suggested that differences between higher and lower VVI individuals might be specifically related to the way in which MR is accomplished rather than how well the MR task is performed [6] [7]. If this is the case, higher and lower VVI individuals might perform equally well in the

letter MR task, but still show systematic differences between the electrophysiological correlates of MR.

Method

Participants

Forty-one students from University of Edinburgh entered this study. All were right-handed and had normal or corrected-to-normal vision. Lower and higher VVI individuals were grouped by a median split of their score to the visual imagery vividness questionnaire (VVIQ-2, [5]). Two individuals with exactly median scores were excluded. Three participants were excluded from data analysis because of excessive noise in the EEG data. The remaining sample consisted of thirty-six participants (19 males; age range 18 - 22 years; mean age: 20.1 years), eighteen higher (nine males; VVIQ = 115.9 ± 8.2) and eighteen lower VVI individuals (nine males; VVIQ = 141.3 ± 8.2).

Stimuli and Procedure

Participants were seated in an electrically shielded, dimly lit, sound attenuating room. The computer monitor was located at a distance of 76cm in front of the participants. On each trial, one of the upper character letters F, L, P and R was presented in white on a black background (3 cm height, subtending 2.26° of visual angle). The letter was presented in its normal or mirror version (standard and mirror letters, respectively) rotated 0°, 30°, 60°, 90°, 120° or 150° degrees clockwise or counter-clockwise from its vertical upright position.

Each trial began with the presentation of a letter for 500ms. After the letter offset, a fixation cross remained on the screen for a variable interval randomly set between 1900 and 2200ms. Letters were presented in blocks of 96 trials (four letters × two stimulus parities × six rotation angles × two rotation orientations). Participants completed 10 blocks in total (960 experimental trials).

Participants were instructed to respond to the parity of the letter (standard vs. mirror) quickly and accurately while maintaining fixation. Two vertically arranged keys were operated by the left and right index fingers. The hands position (left hand on the top key and right hand on the bottom key, and vice-versa) was changed after each block. Throughout the experiment, the top and bottom keys were set for responses to standard and mirror stimuli, respectively. Participants completed 48 practice trials with the letters "G" and "J", before performing the experimental task.

Electrophysiological Recording

EEG was acquired continuously from 64 active electrodes (BioSemi Active Two system) at a sampling rate of 512 Hz. Two electrodes positioned on the left and right ear lobes served as references. The horizontal EOG (hEOG) and vertical EOG (vEOG) were measured from four additional electrodes placed on the outer canthi of the eyes and the sub- and supra-orbital ridges of the right eye, respectively, and were calculated offline as the difference between these electrodes. The EEG signal was digitally re-referenced to the average of the left and right reference electrodes. EEG, hEOG and vEOG were filtered using a 0.53 high pass and a 40 Hz low pass filter and segmented into discrete, single-trial epochs of 850ms from 100ms before to 750 ms after letter onset. Trials with eye blinks (VEOG exceeding $\pm$ 60 μV), horizontal eye movements (HEOG exceeding $\pm$ 80 μV) and other artefacts (EEG amplitudes exceeding $\pm$70 μV at any scalp electrodes) throughout the epoch were excluded from analysis. Participant averages were computed on correct trials for each combination of stimulus parity (standard, mirror) and rotation angle (0°, 30°, 60°, 90°, 120°, 150°). Data from trials with different letters and different directions of rotation (clockwise, counter-clockwise) were collapsed across.

Electrophysiological Data Analysis

The RRN component was computed by subtracting ERPs elicited on trials in which the letter was presented in the upright position (at 0°) from those elicited on trials in which the letter was shown at different rotation angles (30°, 60°, 90°, 120°, 150°), separately for standard and mirror letters. ERP waveforms measured from central and parietal electrodes (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) where the RRN was observed in previous ERP studies of MR [9] were pooled together.

The RRN amplitude was measured in two consecutive time windows between 350 and 500ms and between 500 and 650ms respectively and submitted to mixed ANOVAs with VVI (higher and lower VVI individuals) as between-subject factor and stimulus parity (standard or mirror) and rotation angle (30°, 60°, 90°, 120°, 150°) as within-subject factors[1].

Main effects or interactions involving the factor rotation angle were further assessed by polynomial contrasts and trend analyses. The MR slopes of the regression function relating RRN amplitudes to rotation angles (MR slopes of RRN amplitude) were calculated and compared between different experimental conditions/groups where necessary. Furthermore, independent *t*-tests (two-tailed) were carried out to investigate differences between consecutive rotation angles. Bonferroni corrections were applied wherever appropriate. Greenhouse-Geisser corrections were used in case of sphericity violations. Partial η^2-values were reported throughout.

To test the presence of group differences in the onset/offset of the RRN component[2], we followed the Jackknife procedure [23] which has been used before to compare the time-course

[1]Preliminary analyses were carried out including the factor hemisphere (left- vs, right-central-parietal sites, pooled over Cp1, Cp3, P1, P3, and Cp2, Cp4, P2, P4 respectively). Because no relevant interaction involving this factor was observed in any of the time windows, all *p*-values $> .05$, it was not included in the final analyses.

[2] To investigate the duration of the RRN component elicited on different rotation angle trials, we applied the Jackknife procedure to the RRN measured in all participants (regardless of VVI group), separately for each stimulus parity (standard and mirror). Because the RRN elicited in the 30° condition of standard trials was extremely shallow, it was problematic to extract a reliable measure of its peak. Thus, it was excluded from this analysis. Repeated-measures ANOVA were carried out on the

of the RRN component [19], [11], [24]. This approach increases the power in the analysis of ERP components' onset/offset while controlling for the Type I error [23], [25]. The Jackknife-averaged RRN were calculated separately for each group, angle and stimulus parity through an iterative procedure in which averages were computed from subsamples in which a different participant was excluded from the original sample on each iteration [23]. The onset/offset latencies were estimated by examining when the RRN amplitudes reached 50% of its maximum amplitude within a 300-750ms post-stimulus time window (in line with the parameters used by Heil and Rolke [11]). Independent t-tests were used to compare latencies differences across groups, separately for each rotation angle with corrections suggested for Jackknife-based scoring in factorial design [24].

Behavioural Data Analysis

Trials with different orientations (clockwise and counter-clockwise) and with different letters (F, L, P and R) were combined for each rotation angle and each stimulus parity for analyses. RTs exceeding two standard deviations above or below the mean, calculated separately for each participant and each experimental condition, were excluded (4.6% of the trials on average). Mixed ANOVAs were conducted with VVI (lower and higher VVI individuals) as a between-subject factor and rotation angles (0°, 30°, 60°, 90°, 120°, 150°) and stimulus parity (standard or mirror) as within-subject factors. Main effects and interactions involving the factor rotation angle were further assessed by trend analyses (only significant trends were reported). Whenever a linear trend was observed for rotation angle, the MR slopes

onset, offset and duration of the RRN with rotation angle as a within-subject factor (60°, 90°, 120° and 150°). For standard stimuli, there was no main effect of angle on the RRN onset, Fc (3, 105) = 1.0, pc = .4, while both offset and duration were modulated by rotation angle (Fc (3, 105) = 24.5, pc < .001 and Fc (3, 105) = 3.28, pc = .02, respectively). For mirror stimuli, main effects of rotation angle were observed on the onset, offset and duration of the RRN, all F_cs ≤ 6.2, all p_cs ≤ .001. This suggests that the duration of the RRN increases with rotation angles, in line with the hypothesis that this component reflects the duration of MR.

and intercepts of RTs were calculated and compared between different experimental conditions or between different VVI groups, as appropriate.

Results

Behavioural Results

Response Times

The main effect of *stimulus parity*, F (1, 35) = 73.01, p< .001, η^2= .68, revealed that RTs were slower on mirror (M = 601.62ms, SE = 16.54) than standard letters trials (M = 671.67ms, SE = 18.88). The main effect of *rotation angle* was also significant (F (5, 175) = 170.39, p<.001, η^2= .83) and was described by both linear (F (1, 34) = 216.02, p< .001, η^2= .86) and quadratic (F (1, 35) = 68.28, p< .001, η^2= .67) trends. RTs associated with each two consecutive rotation angles differed significantly from each other (all ps < .001).

In addition, a significant *rotation angle* × *stimulus parity* interaction was present, F (5, 175) = 5.05, p= .004, η^2= .13. Follow-up analyses were conducted separately for standard and mirror letter trials. In the standard condition, the main effect of rotation angle, F (5, 175) = 253.23, p < .001, η^2 = .88, was described by a linear (F (1, 35) = 324.75, p <.001, η^2 = .91), quadratic (F (1, 35) = 117.52, p < .001, η^2 = .78) and cubic trends (F (1, 35) = 12.49, p = .001, η^2= .27). Significant differences in RTs emerged in any two consecutive angles (all ps ≤ .003). In the mirror condition, the main effect of rotation angle was present, F (5, 175) = 91.38, p< .001, η^2= .73, and could be described by a linear (F (1, 34) = 130.56, p < .001, η^2= .79) and a quadratic trend (F (1, 35) = 23.8, p < .001, η^2 = .41). The rate of MR was faster for mirror (M = 1.45ms/degree; SE = .13) than standard stimuli (M = 1.61ms/degree, SE = .9), as revealed by the analysis of the MR slopes of RTs (F (1, 35) = 5.55, p = .024, η^2 = .14). In addition, a smaller intercept was observed for standard (M = 480.52ms, SE= 12.1) than for mirror letters (M = 563.18ms, SE = 15.0), F (1, 35) = 76.74, p < .001, η^2 = .69.

Although lower VVI individuals (M = 662.43ms, SE = 24.4) were numerically slower than higher VVI individuals (M = 610.86ms, SE = 24.4), there was no statistically significant difference between these two groups in the RT analysis, F (1, 35) = 2.23, p= .145. No other interactions involving VVI emerged to be significant (all Fs < 1.61, all ps > .159).

Accuracy

The main effect of *stimulus parity*, F (1, 35) = 4.79, p= .036, η^2 = .12, showed that accuracy rates were higher for mirror (M = 94.5%, SE = 1.0) than standard letters (M = 93.3%, SE = .9). There was also a significant main effect of *rotation angle*, F (5, 175) = 34.1, p< .001, η^2= .50. Pair-wise comparisons carried out between successive angles showed that accuracy rates decreased significantly between 60° and 90° (from 96.2% (SE = .7) to 94.8% (SE = .7), p= .050, d =.35, and between 120° and 150° (87.0%, SE = 1.8), p < .001, d = .75. Accuracy rates gradually decreased with increasing rotation angles, as suggested by a linear (F (1, 35) = 45.44, p < .001, η^2 = .57), a quadratic (F (1, 35) = 28.86, p< .001, η^2= .46) and a cubic trend (F (1, 34) = 14.97, p< .001, η^2 = .306).

In addition, *rotation angles* interacted with *stimulus parity*, F (5, 175) = 9.45, p = .002, η^2 = .22. In the standard condition, a main effect of rotation angle, F (5, 175) = 27.76, p < .001, η^2 = .45, revealed that the accuracy decreased with increasing rotation angles as described by linear (F (1, 35) = 29.48, p< .001, η^2= .46), quadratic (F (1, 35) = 30.34, p < .001, η^2= .47) as well as cubic trends (F (1, 35) = 14.92, p < .001, η^2 = .31). Responses to 150°-rotated standard letters (M = 81.5%, SE = 2.9) were less accurate than those to 120°-rotated stimuli (M = 91.8%, SE = 1.6), p< .001. However, no main effect of rotation angle emerged on mirror trials, F (5, 175) = 1.35, p= .246, η^2= .04.

No statistical difference emerged between the accuracy rates of lower and higher VVI individuals (Lower VVI: M = 93.3%, SE = 1.3; Higher VVI: M = 94.5%, SE = 1.3), F (1, 35)

= .42, p= .522. In addition, no interactions involving the factor VVI were observed on the accuracy rates (all Fs < .95, all ps > .36).

Electrophysiological Results

The main effect of *rotation angle* was present in both 350-500ms (F (4, 140) = 37.44, p< .001, η^2= .52) and 500-650ms (F (4, 140) = 24.13, p < .001, η^2= .42) time windows. As shown in Fig.1, RRN amplitudes became more negative with the increasing rotation angles in both time windows and followed a linear trend only (350-500ms: F (1, 35) = 71.25, p< .001; 500-650ms: F (1, 35) = 12.41, p < .001, η^2= .27). Further post-hoc comparisons contrasting the RRN amplitudes for successive rotation angles revealed that MR effort (increased RRN amplitude for the larger rotation angle) was reliably present for smaller rotation angles (30°-60°: p <.001; 60°-90°: p = .004) in the early RRN time window (350-500ms), whereas in the late RRN time windows (500-650ms) these differences were evident for larger rotation angles (90°-120°: p = .010, 120°-150°: p < .001).

There was no main effect of *stimulus parity* between 350 and 500ms post-stimulus, F (1, 35) = .54, p = .469. This main effect was present in the 500-650ms time window, F (1, 35) = 43.31, p<.001, η^2= .56, revealing larger RRN amplitudes in the mirror (M = 1.36μV, SE = .17) compared to the standard condition (M = -.20μV, SE = .24).

In the 350-500ms interval, there was a significant interaction between *rotation angle* and *stimulus parity*, F (4, 140) = 14.61, p < .001, η^2 = .30. Main effects of rotation angle were present for both standard (F (4, 140) = 46.63, p < .001, η^2= .58) and mirror stimuli (F (4, 140) = 7.11, p < .001, η^2 = .17). In the standard condition, significant RRN amplitude differences were found in the following two consecutive angles: 30°-60° (p = .008), 60°-90° (p = .009) and 90°-120° (p= .012). In the mirror condition, RRN differences were only present between 30° and 60° (p = .030). In both cases, the RRN amplitude became more negative with

increasing rotation angles and followed a linear trend (standard: F (1, 35) =115.85, $p < .001$, $\eta^2 = .77$; mirror: F (1, 35) = 12.41, $p = .001$, $\eta^2 = .27$). The subsequent analysis of the MR slopes of RRN amplitudes showed a more pronounced RRN in the standard (M = -.023μV/degree, SE = .002; see Fig.1, left panel) than in the mirror condition in this interval (M = -0.008μV/degree, SE = .002; Fig.1, right panel), F (1, 34) = 44.84, $p < .001$, $\eta^2 = .57$.

In the 500-650ms time window, stimulus parity did not interact with rotation angle, F (2.8, 94) = 2.57, $p = .064$.

No main effect of *VVI* or related interactions emerged in the early RRN time window (350-500m). By contrast, differences between imagery abilities groups emerged in the late RRN interval (500-650ms), F (1, 35) = 4.33, $p = .045$, $\eta^2 = .11$, revealing larger RRN amplitudes in lower (M = .93μV, SE = .24) than in higher VVI individuals (M = .23μV, SE = .24).

Moreover, a three-way interaction between *VVI*, *stimulus parity* and *rotation angle* was present between 500 and 650ms post-stimulus, F (4, 140) = 3.53, $p = .021$, $\eta^2 = .09$. Follow-up analyses were conducted separately for the standard and mirror conditions. The *group* × *rotation angle* interaction was present for standard letters (Fig.1, left panel), F (4, 140) = 3.7, $p = .021$, $\eta^2 = .10$. In higher VVI individuals, the main effect of rotation angle, F (4, 140) = 3.35, $p = .042$, $\eta^2 = .16$, revealed that the RRN amplitudes were significantly larger at 150° as compared to 120° ($p = .029$), whereas no difference emerged between any other two consecutive angles, all ps ≥ .58. Trend analyses confirmed that the RRN amplitudes in higher VVI individuals followed a quadratic trend only, F (1, 17) = 13.48, $p = .002$, $\eta^2 = .44$. In lower VVI individuals, the main effect of rotation angle was also evident, F (4, 140) = 16.08, $p < .001$, $\eta^2 = .49$. The RRN amplitudes were significantly larger at 150° as compared to 120° ($p = .019$) and the difference between 90° and 120° approached significance ($p = .064$). RRN

amplitudes in lower VVI individuals followed both linear, F (1, 17) = 31.74, $p < .001$, $\eta^2 = .65$, and quadratic trends, F (1, 17) = 4.78, $p = .043$, $\eta^2 = .22$. In the mirror condition, there was no interaction between imagery vividness and rotation angle[3], F (4, 140) = .86, $p = .44$.

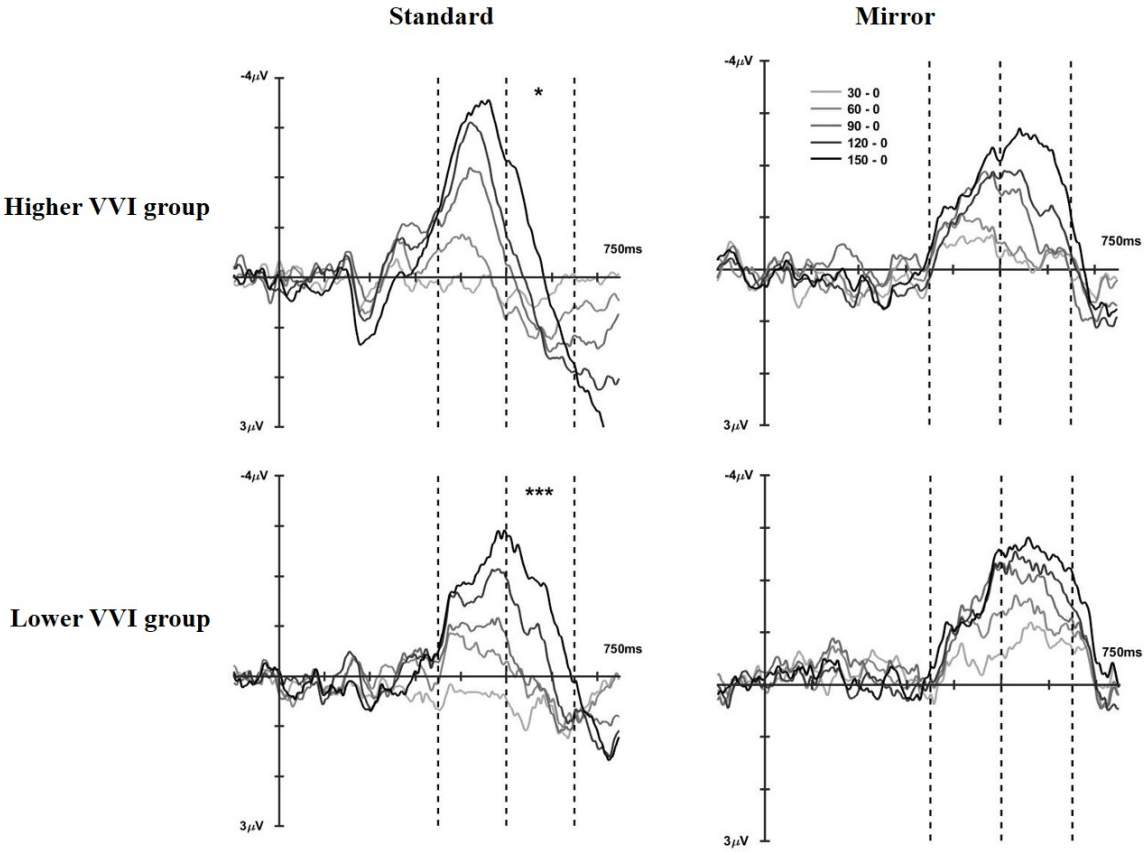

Figure 1 RRN elicited over pooled central-parietal sites Cpz, Cp1/2, Cp3/4, Pz, P1/2 and P3/4 in individuals with lower and higher VVI (top and bottom panels) during the mental rotation of standard and mirror letters (left and right panels).

[3] To characterize the RRN elicited by mirror stimuli in the 500-650 ms time window, further analyses were conducted separately for each VVI group. Main effects of rotation angle were present in both higher (F (2.3, 38.2) = 13.66, $p < .001$, $\eta^2 = .45$) and lower VVI individuals (F (2.1, 36.2) = 6.3, $p = .004$, $\eta^2 = .27$), revealing that RRN amplitudes became more negative with increasing rotation angles. RRN amplitudes followed both a linear and a quadratic trend for higher VVI individuals, but were linearly correlated with rotation angle only in lower VVI individuals.

Onset and Offset of the RRN component

As shown in Fig. 2, the duration of the RRN is longer in individuals with lower than higher VVI. This is particularly evident for standard letters with larger rotation angles (90°, 120°, and 150°).

Standard Letters

Results revealed no significant difference on the onset of the RRN elicited by standard letters in the lower and higher VVI group in all rotation angles, all t_c (34)s $\leq$ .67, p_cs $\geq$ .25.

Group comparisons carried out on the offset latencies of the RRN separately for each rotation angle revealed delayed RRN offset for lower as compared to higher VVI individuals. This delay was observed for the 90°, (t_c (34) = -2.76, p_c = .005; higher VVI = 473.97ms, SE = 2.32; lower VVI = 504.68ms, SE = 1.52), 120°, (t_c (34) = -3.27, p_c = .001;higher VVI = 478.74ms, SE = 3.41; lower VVI = 532.67ms, SE = 2.30) and 150° rotation angles (t_c (34) = -2.00, p_c = .027; higher VVI = 531.80ms, SE = 2.98; lower VVI = 594.52ms, SE = 3.01). No group difference was present for the 30° (t_c (34) = -.24, p_c = .41) and 60° (t_c (34) = -.08, p_c = .46) rotation angles.

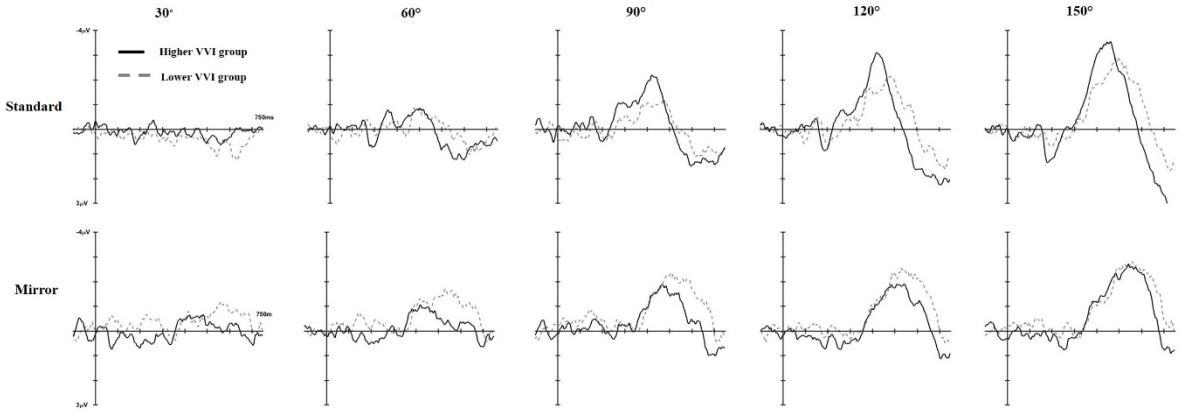

Figure 2 RRN elicited by standard and mirrored letters in higher and lower VVI individuals shown separately for each rotated angle (30°, 60°, 90°, 120° and 150°).

Mirror Letters

The onset latency of RRN was delayed in individuals with lower as compared to higher VVI in mirror letters presented with 30°, t_c (34) = -1.84, p_c = .037 (lower = 408.43ms, SE = 4.83; higher = 368.17ms, SE = 2.53), and 60° rotation angles, t_c (34) = -1.74, p_c = .046 (lower = 388.03ms, SE = 3.21; higher = 364.16ms, SE = 1.20). This group difference was not present in the other rotation angles (90°, 120° and 150°), all t_c (34)s $\leq$ .69, p_cs $\geq$ .75

Group comparisons carried out on the RRN offset revealed no group difference in any of the rotation angles, all t_c (34)s $\leq$ 1.60, p_cs $\geq$ .06, expect for the 30° (t_c (34) = -2.28, p_c = .015) where the RRN offset was delayed in individuals with lower (M = 665.16ms, SE = 19.12) as compared to higher VVI (M = 490.14ms, SE = .81).

Discussion

To investigate whether differences in the VVI are reflected by differences in the electrophysiological correlate of MR, the RRN component, we asked individuals with lower and higher VVI to complete a classic letter rotation task. We observed systematic RRN differences between lower and higher VVI groups. Specifically, the duration of the pure MR process was longer in individuals with lower VVI as compared to those with higher VVI for standard letters, as revealed by the fact that the onset of the RRN component was similar across groups but its offset was delayed in lower VVI individuals. This delay was observed for larger rotation angles (90°, 120° and 150°), but not for smaller angles (30° and 60°). This is likely due to the fact that when presented with familiar stimuli (standard letters) at small rotation angles participants are able to identify them without fully engaging with MR processes as suggested by the curvilinear trend in RTs reported in the existing literature [19].

The VVI group difference in the time course of the RRN was also reflected in the analysis of the mean RRN amplitudes. In the 500-650ms time window, encompassing the late phase of the RRN component, larger amplitudes were observed for lower than higher VVI individuals. In lower VVI individuals, the RRN amplitude increased linearly with increasing rotation angles, suggesting that the MR proper was still executed in this time window. By contrast, in the higher VVI group, the RRN amplitude in the different rotation angles was better described by a quadratic trend, revealing that the MR of small rotation angles letters was almost completed. These findings suggest that the RRN amplitudes were reduced in higher compared to lower VVI individuals in the late RRN time window. This difference may be due to individuals with higher VVI completing MR processing earlier than those with lower VVI. That is, the amplitude differences between groups are likely to be driven by longer rotation processes rather than an increased rotation effort in individuals with low VVI.

Group differences in both the amplitude and latency of the RRN were observed during the rotation of standard stimuli. As shown in Fig. 2, a similar pattern of group differences was present for mirror letters, however this was not systematically detected by statistical analyses. Rotating mirror letters is more cognitively demanding than rotating standard letters [19], which increases the variability of MR processes across trials and across individuals. Because the RRN component is time-locked to the onset of MR process [11], this ERP component becomes smeared when the MR processes are engaged at different times on different trials due to the averaging process [17] (see Fig. 2 for differences in peak sharpness between standard and mirror letters). This increased trial-by-trial variability may prevent the detection of reliable peaks, resulting in a lack of group differences in the mirror condition.

Our results reveal systematic groups differences in the RRN observed in the standard condition. How can variations in the VVI explain the differences in the timing of MR process? The precision of the visual representation is correlated with the speed of MR: more precise visual representations are associated with a faster execution of the MR process (e.g. [26]). In addition, the MR rate is also modulated by the amount of information stored in mental representations, as suggested by slower MR processes when the visual representations contain more information [27], [28]. The content (amount of information extracted) and accuracy of the visual representation varies across individuals [28], [29], [30]. Higher VVI individuals are capable to create and maintain more accurate visual representations [29] and might therefore be able to complete the MR process faster than lower VVI individuals. However, individuals with higher VVI are also able to adapt the amount of information retained during MR, simplifying the content of the visual representation whenever necessary [6]. It is therefore possible that higher VVI individuals are able to create simplified visual representations (i.e. rotation-related information [27]) that can be easily rotated. By contrast lower VVI individuals may encode additional but unnecessary information which might extend the rotation process.

Despite the fact that ERP results consistently suggested an extended rotation process for lower compared to higher VVI individuals, this difference was not present in the behavioural measures (RTs or accuracy rates). It is possible that the letter rotation task used here is too easy to elicit consistent differences in performance between groups. It is also possible that the prolonged duration of MR process proper in lower VVI individuals was compensated by a reduced duration of subsequent cognitive processes, resulting in no imagery vividness discrepancies in the behavioural measures which reflect the end result of different cognitive processes.

Recent evidence [21] showed that poor performance in a classic letter rotation task was associated with increased RRN amplitudes, suggesting that low-performers increased their MR effort to cope with the MR task. The current results provide converging evidence that the ability to create and transform visual mental representations varies considerably across individuals, as indicated by the fact that the MR process was prolonged in lower relative to higher VVI individuals. Crucially, however, in the present study participants were grouped according to their VVI (as measured by the VVIQ questionnaire, [5]). While generally self-report measures are prone to biases, VVIQ scores are correlated with the activation of the early visual cortex relative to the whole brain activity during imagery tasks [31]. Results of the present study revealed that individuals with lower VVI were not 'lower performer' (i.e. accuracy and RTs were comparable across higher and lower VVI groups). This suggests that VVI impacts on '*how'* rather than *'how well'* MR rotation is accomplished. In line with existing evidence [7] brain imaging methods can highlight subtle individual differences between higher and lower VVI individuals that would not be evident with behavioural measures alone. This could at least in part explain why some studies have failed to observe differences in the behavioural performance of individuals with higher and lower VVI during MR tasks, contributing to the current debate concerning whether the VVI is related to mental-rotation ability (e.g. [9], [10]).

Funding:

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Reference

[1] R.N. Shepard, J. Metzler, Mental rotation of three-dimensional objects, Science, 171 (1971), pp. 701-703

[2] R.N. Shepard, L. A. Cooper, Mental images and their transformations, MIT Press, Cambridge, MA, 1982.

[3] L.A. Cooper, R.N, Shepard, Chronometric studies of the rotation of mental images, in: W.G. Chase (Ed.), Attention & Performance IX, Erlbaum, N.J. Hillsdal, 1973, pp. 75-176.

[4] R.R. Reeder, Individual differences shape the content of visual representations, Vision research, 141, (2017), pp.266-281.

[5] D.F. Marks, Consciousness, mental imagery and action. British Journal of Psychology, 90 (1999), pp. 567-585.

[6] B. Zhao, S. Della Sala, Different representations and strategies in mental rotation, Quarterly Journal of Experimental Psychology, 71 (2018), pp. 1574-1583.

[7] R.H. Logie, C.R. Pernet, A. Buonocore, S. Della Sala, Lower and higher imagers activate networks differentially in mental rotation, Neuropsychologia, 49 (2011), pp. 3071-3077.

[8] A.Z. Zeman, S. Della Sala, L.A. Torrens, V.E. Gountouna, D.J. McGonigle, R.H. Logie, Loss of imagery phenomenology with intact visuo-spatial tasks performance: a case of 'blind imagination', Neuropsychologia, 48 (2010), pp. 145-155.

[9] S. E. Poltrock, P. Brown. Individual differences in visual imagery and spatial ability, Intelligence, 8 (1984), pp. 93-138.

[10] H. Habacha, C. Molinaro, F. Dosseville, Effects of gender, imagery ability, and sports practice on the performance of a mental rotation task, The American Journal of Psychology, 127 (2014), pp. 313-323.

[11] M. Heil, B. Rolke, Toward a chronopsychophysiology of mental rotation, Psychophysiology, 39 (2002), pp. 414-422.

[12] I.M. Harris, C. Miniussi, Parietal lobe contribution to mental rotation demonstrated with rTMS, Journal of Cognitive Neuroscience, 15 (2003), pp. 315-323.

[13] M. Heil, J. Bajrić, F. Rösler, E. Hennighausen, Event-related potentials during mental rotation: disentangling the contributions of character classification and image transformation, Journal of Psychophysiology, 10 (1996), pp. 326-335.

[14] J.M. Zacks, Neuroimaging studies of mental rotation: a meta-analysis and review, Journal of Cognitive Neuroscience, 20 (2008), pp. 1-19.

[15] F. Peronnet, M.J. Farah, Mental rotation: an event-related potential study with a validated mental rotation task, Brain and Cognition, 9 (1989), pp. 279-288.

[16] A.A. Wijers, L.J. Otten, S. Feenstra, G. Mulder, L.J. Mulder, Brain potentials during selective attention, memory search, and mental rotation, Psychophysiology, 26 (1989), pp, 452-467.

[17] M. Heil, The functional significance of ERP effects during mental rotation. Psychophysiology, 39 (2002), pp. 535-545.

[18] H.R. Liesefeld, H.D. Zimmer, The advantage of mentally rotating clockwise, Brain and Cognition, 75 (2011), pp.101-110.

[19] J.P. Hamm, B.W. Johnson, M.C. Corballis, One good turn deserves another: an event-related brain potential study of rotated mirror-normal letter discriminations. Neuropsychologia, 42 (2004), pp. 810-820.

[20] M. Heil, The functional significance of ERP effects during mental rotation. Psychophysiology, 39 (2002), pp. 535-545.

[21] C. Beste, M. Heil, C. Konrad, Individual differences in ERPs during mental rotation of characters: Lateralization, and performance level, Brain and Cognition, 72 (2010), pp. 238-243.

[22] A.C. Neubauer, A. Fink, Intelligence and neural efficiency, Neuroscience & Biobehavioral Reviews, 33 (2009), pp. 1004-1023.

[23] J. Miller, T. Patterson, R. Ulrich, Jackknife-based method for measuring LRP onset latency differences, Psychophysiology, 35 (1998), pp. 99-115.

[24] R. Ulrich, J. Miller. Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs, Psychophysiology, 38 (2001), pp. 816-827.

[25] A. Kiesel, J. Miller, P. Jolicoeur, B. Brisson, Measurement of ERP latency differences: a comparison of single-participant and jackknife-based scoring methods, Psychophysiology 45 (2008), pp. 250–274.

[26] R.J. Mumaw, J.W. Pellegrino, R.V. Kail, P. Carter, Different slopes for different folks: process analysis of spatial aptitude, Memory & Cognition, 12 (1984), pp. 515-521.

[27] H.R. Liesefeld, H.D. Zimmer, Think spatial: the representation in mental rotation is nonvisual, Journal of Experimental Psychology: Learning, Memory and Cognition, 39 (2013), pp. 167-182.

[28] H.R. Liesefeld, X. Fu, H.D. Zimmer, Fast and careless or careful and slow? Apparent holistic processing in mental rotation is explained by speed-accuracy trade-offs, Jounral of Experimental Psychology: Learning, Memory and Cognition, 41 (2015), pp. 1140-1151.

[29] D.F. Marks, Visual imagery differences in the recall of pictures, British Journal of Psychology, 64 (1973), pp. 17-24.

[30] R.R. Reeder, Individual differences shape the content of visual representations, Vision Research, 141 (2017), pp. 266-281.

[31] X. Cui, C.B. Jeter, D.Yang, P.R. Montague, D.M. Eagleman, Vividness of mental imagery: individual variability can be measured objectively, Vision Research, 47, (2006), pp.474-478.